

herpes virus capsids [19] can be inhibited by the presence of non-polymerizable actin or depolymerization of F-actin.

It is unclear from these studies just how direct the requirement for actin in transport within nuclei is, but it is reasonable to suppose that directed transport would be important in a massive nucleus such as that of an amphibian oocyte, with a volume ~25 000 times larger than that of a typical somatic cell. Intriguingly, a recent ultrastructural study [20] of isolated *Xenopus* oocyte nuclei observed filaments, which could be decorated with anti-actin antibodies and which were sensitive to actin depolymerizing drugs, connecting nuclear pore complexes to intranuclear structures like nucleoli.

We are just beginning to understand forms and functions of nuclear actin. Bohnsack *et al.* [1] have unraveled why actin is allowed in nuclei of *Xenopus* oocytes and showed that it can form a crosslinked filamentous structure in them. It remains to be shown, however, which fibrous actin structures can be found in nuclei of different cells *in vivo* and what their molecular functions are — exciting questions for future research.

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Gene Expression and Cell Biology/
Biophysics Units, European Molecular
Biology Laboratory (EMBL),
Meyerhofstrasse 1, D-69117 Heidelberg,
Germany.
E-mail: jan.ellenberg@embl.de

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Social Learning: Ants and the Meaning of Teaching

Recent research on ants shows that running in tandem might serve the function of teaching naïve ants about the path to a target. Although these new experiments represent perhaps the most highly controlled study of teaching in animals to date, the findings prompt the question of how teaching formally differs from other forms of communication.

Ellouise Leadbeater,
Nigel E. Raine and Lars Chittka

Learning from others is so fundamental to humans that we actively speed up the social learning process — we teach. Non-human animals can also learn from members of their own species, and they might be expected to accrue considerable inclusive fitness benefits by ‘coaching’ kin to

facilitate the rapid development of adaptive behaviour [1–3]. Surprisingly, however, convincing demonstrations of teaching behaviour in animals are rare.

Caro and Hauser [4] laid out the following minimum criteria for information transfer between animals to be classified as teaching. The animal that conveys information must incur a cost, or at least not reap an immediate benefit

from the subsequently altered behaviour of the receiver. The candidate behaviour has to be performed only when uninformed individuals are present. Hence, although juvenile songbirds learn their songs by listening to adult males, the adult is not teaching because he will sing irrespective of the youngsters’ presence. Finally, the teaching must lead the pupil to learn a skill, or acquire knowledge that it would not otherwise obtain, or at least that it would take longer to acquire.

Perhaps the most convincing candidates for teaching among vertebrates involve carnivores learning to hunt (reviewed in [4,5]). Mother cheetahs that would normally capture and kill prey without delay bring live prey back to the nest when their cubs are very

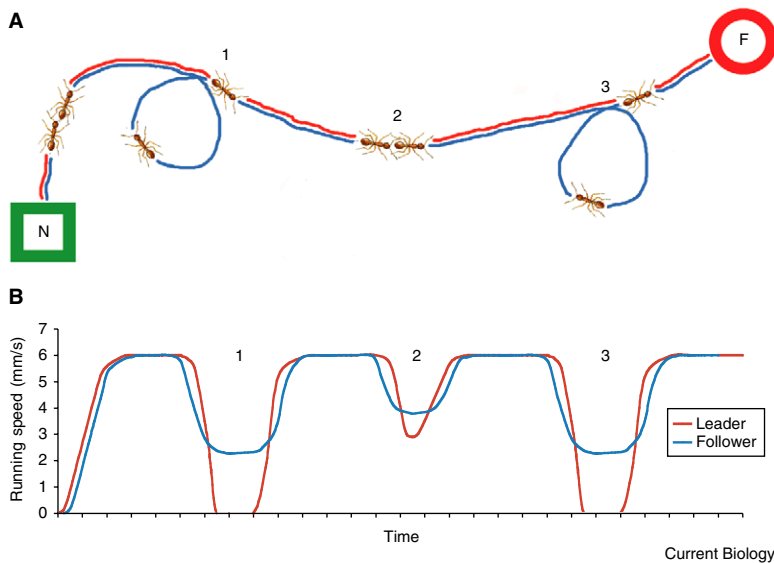


Figure 1. Tandem-running by *Temnothorax albipennis* ants.

(A) Schematic view of path taken by a tandem-running pair of *Temnothorax albipennis* ants from their nest (N) to a food source (F). (B) Running speed of leader (red line) and follower (blue line) during the same tandem-run. Tandem leaders have experience of the food source, whilst followers are naïve of its location. The leader proceeds towards the food source (red path) so long as the follower (blue path) maintains regular antennal contact with the leader's legs or abdomen. Progress of the tandem pair is slowed by frequent periods when the leader remains still whilst the follower performs a looped circuit, possibly to memorise landmarks along the path (points 1 and 3) [8]. Once this exploratory circuit is complete, and the follower re-establishes antennal contact, the leader continues onwards towards the food. If contact between follower and leader becomes less frequent during a tandem-run, the leader will slow down to allow the follower to catch up (point 2).

young. Prey is killed by the mother in front of the cubs. Later, when the cubs begin accompanying her on hunting trips, the mother releases prey in front of them, which the cubs attempt to catch, sometimes at the cost of losing the prey altogether [6]. The cubs' predatory skills improve over this period, although it remains to be shown that this results directly from such practice (the same applies in a study on domestic cats [7]). Other potential cases of teaching involve chimpanzees learning to use stone hammers and anvils, and ospreys teaching their offspring to snatch fish from the water [4,5], but as yet these rely only upon weak anecdotal evidence.

In contrast, Franks and Richardson's [8] well-controlled study on tandem-running *Temnothorax* ants was carried out in a laboratory. The intimate interaction between leader and follower in a pair of tandemly running ants at first sight bears all the hallmarks of a parent teaching a child to ride a bicycle. An experienced ant will lead individual

naïve nest mates to newly discovered food sources or nesting sites, stopping if the follower loses regular antennal contact [9]. When the pair becomes separated, as occurs when the follower makes looping movements possibly searching for landmarks, the leader remains still, only continuing towards the food when the follower has completed her exploratory circuit (Figure 1). Franks and Richardson [8] demonstrate that there are clear two-way interactions between the tandem-running ants. When the gap between them becomes too large, and antennal contact between the pair is lost, the leader slows down and the follower accelerates to catch up. This bidirectional feedback loop appears to maximise the speed at which the two can progress, while allowing the follower to memorise the path and its surrounding landmark features.

Such tandem-running meets most of the criteria for teaching set out in the definition given by Caro and Hauser [4]. When alone, the

leader does not incorporate the frequent pauses which are used by the follower to perform orientation loops. Hence the leader's behaviour is clearly modified in the presence of a naïve observer. Leaders incur a time cost: when an experienced forager is not leading a follower, she travels faster to the food source and does not stop en route [8]. As a result, the follower (pupil) finds the target more quickly than she would do if searching for it alone. While it appears likely that followers learn route-specific information during tandem-running, it remains to be shown empirically precisely what information is obtained.

Franks and Richardson [8] refine Caro and Hauser's [4] working definition of teaching by introducing an additional criterion: that feedback from the learner to the experienced individual must be demonstrated. Such feedback clearly distinguishes tandem-running from other forms of signalling in ants, such as scent-marking food sources, or releasing alarm pheromones in the presence of nest intruders [9]. In these cases, both the signal and the response are largely hard-wired; and there is no need to assume that learnt information has been transmitted, nor is there a need to invoke learning to explain the receiver's response. Most simple forms of signalling, such as use of pheromones, do not appear to meet several criteria laid out by Caro and Hauser's teaching definition: such signals are displayed irrespective of the presence of a naïve receiver, and do not lead to the long lasting changes of receiver behaviour that would qualify as learning [10,11]. So the additional criterion of feedback from the taught individual seems unnecessary. Responding to feedback from pupils makes for more efficient teaching, but teaching, albeit perhaps at a lower quality, can still occur in the absence of such feedback.

In contrast, tandem-running in ants, just like dancing in honeybees, is a much more advanced form of communication. These behaviours specifically

transmit learnt knowledge with flexible information content: in the honeybee dance, for example, any location within the flight range of the colony can be encoded. The acquired information can subsequently be used by newly informed individuals in a manner that is temporally — and, in the case of a honeybee dance, spatially — separated from the information transfer event (Figure 2). This underlines the notion that invertebrates, despite their often miniscule brains, might not be fundamentally different from vertebrates in the types of information processing of which they are capable [12], perhaps the difference is just in the amount of information that can be stored and processed in parallel.

But however impressive these insect forms of social learning may be, we argue that they do not constitute forms of teaching. Our reservations relate to the types of information that are being communicated. Tandem-running ants and dancing bees transfer information about a location of interest. While the mode of information transfer is different, the content is equivalent to humans informing each other about the location of a good restaurant: you tell, not teach, someone its location. In a similar vein, parents helping their children with mathematics homework could simply tell them the answer. But a parent might also teach the child how to work out the solution, rather than to simply tell them what it is. Felids that teach their offspring to hunt facilitate the learning of an ability to perform actions — a skill. In more formal terms, we suggest that teaching should be reserved for transfer of skills, concepts, rules and strategies — not simply the handing over of declarative information (facts), or simple procedural information (such as how to get to a place, by guiding other individuals there).

Caro and Hauser's [4] definition classifies both types of behaviour as teaching. Nonetheless, the two have different functional consequences. Transferring basic information is a solution to a problem in one context, but teaching a skill allows the recipient



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Figure 2. Honeybee waggle dancer surrounded by potential recruits.

Successful honeybee foragers use a ritualised and abstract communication system to convey distance and direction information of a food source to their nest mates in the darkness of the hive [13,14]. The dancer transmits learnt information with a flexible information content: she communicates the location of a profitable foraging site which she herself has learnt. The potential recruits, shown in a semi-circle behind the dancer, can subsequently use the information conveyed by the dancer when they leave the hive and locate the food source she indicated. Whilst this is an impressive feat of directed information transfer, we suggest this does not represent true teaching: the dancer is telling, rather than teaching, the recruits where to go to find food. (Photo by Scott Camazine.)

to solve the problem in multiple situations. When describing teaching in humans we sometimes fail to differentiate; a history teacher may tell a pupil a fact, such as when a war took place, and still be said to be teaching. When considering the evolution of teaching behaviour, however, rigorous terminology allows us to understand differences in the adaptive benefits that transferring knowledge and transferring skills may afford: thus it appears useful to reserve distinct terms for distinct types of information exchange between animals.

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School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK.
E-mail: n.e.raine@qmul.ac.uk

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